Explanation of Plate 8

Fig. 1. *Guianadesma sinuosum,* diagram of gross anatomy of a paratype. AA, anterior adductor muscle. B, byssus. BP, byssal pit. CG, cerebral ganglia. CST, crystalline style sac. ES, excurrent siphon. F, foot. G, gill. H, heart. INT, intestine. IS, incurrent siphon. LN, ligamental notch. LP, labial palps. M, mantle. OES, oesophagus. PA, posterior adductor muscle. PER, pericardium. R, rectum. RM, posterior retractor muscle. S, septum. ST, stomach. VG, visceral ganglia.

Figs. 2–6. *Guianadesma sinuosum,* holotype. (3/1). 2, Interior of left valve. 3, Interior of right valve. 4, Ventral view. 5, Exterior of right valve. 6, Exterior of left valve.

VARIABILITY, DEVELOPMENTAL CHANGES, AND DENTICLE-REPLACEMENT IN THE RADULA OF *LYMNAEA STAGNALIS APPRESSA SAY*

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In the course of other researches on *Lymnaea stagnalis appressa* Say carried out in this laboratory certain points on the morphology and functioning of the radula have come to our attention which are worthy of record, because of the importance placed by some workers on radular dentition in taxonomy. These points concern the marked variation in radular pattern in different individuals, the development, wear, loss, and replacement of radular denticles throughout the life of the snail, and the elimination of the discarded teeth through the alimentary tract.

Historical. Hoffmann (1932) described the formation of the radula in *L. stagnalis,* reviewed the controversial issues of earlier writers, and concluded that, once the odontoblastic cushion is built, it is permanent and fixed and each odontoblast produces all of the teeth of one longitudinal row in the radular ribbon. He observed that the part of the radula which has only recently separated from the odontoblastic cushion is soon joined firmly to the subradular epithelium by the secretion of the subradular chitin. He stated also that the radula probably does not pass out over the subradular epithelium by an independent movement, but rather by a relative displacement of the radula out of the radular sac as a consequence of the growth of the entire buccal mass. Cawston (1928, 1930, 1940) asserts that lymnaeids add new rows of teeth from the nascent posterior border of the radula; that the number of tricuspid teeth is increased by coalescence of the cusps of the marginal teeth; that older snails have more rows of worn anterior teeth and also a greater number of total rows of teeth than younger snails; and that shedding of molluscan teeth is a less frequent process than is commonly supposed! He counted 500 teeth in the radula of *Bulinus tropicus* at hatching time, and in a few weeks the number of teeth increased from 7,000 to 10,000, a number which he believed remains fairly constant throughout the life of the snail. Pruvot-Fol (1926) describes the first very small teeth observable on the anterior portion of the radula as the teeth of the preradula, which, she writes, are the first formed set of embryonic cusps and are noted most prominently in Pulmonata. The radulae of other snails have been studied by Bowell (1924) and by Howe (1930, 1938). The latter worked on Pleuroceratidae and found a distinct increase in the size of the teeth concomitant with the increase in size of the shell. He concluded that in this family the radular formulae are not safe criteria for specific diagnosis. He maintained that the size of the snail should always be stated when the radula is to be used for purposes of classification.

Methods. Fresh radulae were dissected from recently killed snails and mounted temporarily in distilled water for study. For permanent radular mounts the radulae were removed from the buccal mass with a minimum of muscle tissue and digested in 10% KOH for one to two days at room temperature. When clean they were rinsed and stained in 1% chromic acid for 10 to 15 minutes, run up through the alcohols including absolute alcohol, and mounted in Seiler's alcohol balsam (Lee, 1937).

By the method of Campbell (1929) the radulae were found to be composed of chitin. Further, after heating in 88% alkali at 160° C. for 15 minutes, and staining, the radulae appeared visibly unchanged, indicating the high content of chitin. Spek (1921) has shown the radulae of *Helix* and of *Arion* to be composed mainly of chitin.

Variation of the Dentitional Pattern. F. C. Baker (1928) gives the radular formula of *L. s. appressa* as follows:

$$\frac{24}{3-4}-\frac{3}{3}-\frac{19}{2}-\frac{1}{1}-\frac{19}{2}-\frac{3}{3}-\frac{24}{3-4}.$$

Examination of 20 radulae of *L. s. appressa* taken from (1) approximately the tenth laboratory generation of snails collected originally in Fox Lake, Wisconsin, (2) recently collected Fox Lake snails, and (3) native snails from Lake Metonga, Wisconsin, has disclosed a wide variation in the radular dentition not indicated by Baker's formula. These 20 snails varied in shell length from 33 to 46 mm. The maximum and minimum numbers of lateral, intermediate, and marginal teeth, respectively, found in the radulae of these snails were as follows: (1) laboratory Fox Lake: 14–19, 2–5, 21–30; (2) native Fox Lake: 18–25, 3–4, 23–28; and (3) native Metonga: 15–25, 1–5, 13–28. F. C. Baker gives the following figures for three different subspecies of *stagnalis: L. s. appressa* (1911, 1928): 19, 3, 24; for the same snail in 1902: 13, 4, 29; *L. s. lillianae* (1928): 15, 8, 16; and for *L. s. sanctaemariae* in the same year: 18, 4, 24.

In almost every transverse row of teeth in the radulae examined the first lateral tooth was distinctly tricuspid, and occasionally some of the other laterals exhibited three cusps. In contrast to this Baker (1928) points out that "No tricuspid first laterals have been seen in any American specimens of this species" (*stagnalis*). There appeared also considerable variation in the number of longitudinal rows of lateral teeth on both sides of the same radula: a difference of three rows was not uncommon, and a maximum difference of seven rows was noted in one case. The average number of intermediate teeth was three. The median unicusp was constant throughout. The number of marginal teeth was usually the same on either side of the same radula. The number of transverse rows of teeth varied in the snails from the different localities: on the average in the native Fox Lake *L. s. appressa* about 100 rows; in the tenth generation laboratory Fox Lake snails, 120; and in the native Lake Metonga snails, 140. The milder environmental conditions in the laboratory may reduce the loss of teeth, and possibly accounts for the greater number of transverse rows of teeth of the laboratory snail over the same snail in its natural habitat. The number of teeth in each transverse row was roughly 100, but varied considerably even in snails of the same length. No deviation was observed in the parallel arrangement of the longitudinal rows of teeth. Evident here and there along the longitudinal rows was the gradual transition of the marginal teeth to the lateral teeth; marked transition in any one radula was not observed, but quite noticeable was the fact that the teeth did not pass gradually and imperceptibly from one form to the other, but that a vacillation occurred in which there appeared a periodic recurrence of the marginal tooth characters; towards the nascent end of the row the recurrence displayed the recapitulation less intensely with each repetition. The dimensions of the radulae varied from 6.0 × 2.5 to 4.0 × 2.0 mm., and there was a fair correlation of radular dimensions with the number of transverse rows of teeth and the number of teeth in the transverse rows.

These radulae exhibited a series of morphological types in each transverse row of teeth. These are listed here beginning with the extreme marginals and leading in to the median tooth: (1) the relatively small and inconspicuous marginal rounded knobs which elongated, becoming quite slender and developed minute cusps; (2) the midmarginals in which the cusps reached their maximum number and then started to decrease again as the tooth shortened; (3) the intermediates where the tooth shortened to the length maintained by the laterals; (4) and finally the laterals in which all of the cusps of the marginals merged (or perhaps became reduced) to the average number of two. The first lateral increased the number of cusps again to three; the median tooth retained the unicuspid condition. Occasionally an entire longitudinal row of lateral teeth was met which was completely unicuspid, indicating, with what has been described above, the general tendency of the teeth to take on the unicuspid shape.

A glance at the numbers of the different kinds of teeth in various specimens of *L. s. appressa*, and in the related subspecies given by Baker, indicates to some extent the marked variation and overlapping of the numerical limits of the different teeth in the radulae of the subspecies of *Lymnaea* represented, and also in the individuals of *L. s. appressa* itself.

Wear, Loss, and Replacement of Teeth. The first nascent posterior transverse row of teeth in these radulae appeared as a vague transparent image; proceeding forward the teeth became gradually transformed into the fully hardened chitinous denticles. The teeth in the first transverse row on the anterior margin of the radula had been reduced to rounded stubs by constant wear. Posteriad for approximately 25 transverse rows the teeth displayed progressively less wear. The anterior border of the radula was rounded and not squared as one might expect from the fact that the teeth in each transverse row are produced simultaneously. The rounding is effected by the earlier loss of the more weakly attached marginal teeth.

Evidence for the fact that teeth are dropped from the radula was found in the examination of fresh radulae and of fecal pellets. In fresh radulae the scars of 4 to 5 denticular plates of attachment in the radular membrane were evident anterior to each of the last attached anterior teeth.

Microscopic examination of the fecal pellets of a normal 40 mm. snail over a period of 23 days showed that a surprisingly large number of radular teeth are dislodged daily, swallowed, and passed out in the fecal material. This snail was isolated in a two-liter glass container containing a half inch mesh paraffined metal screen over the bottom which permitted the feces to collect there undisturbed by the snail; snails commonly consume their own feces. That this snail was a normal one was indicated by the fact that it oviposited three egg capsules and added 2 mm. to the length of its shell during the experiment. Moreover at the conclusion of the experiment, dissection revealed that the radula was normal in all respects. A total of 613 teeth of all types was discarded in 23 days as follows (days in parenthesis): (1) 1, (2) 1, (3) 0, (4) 0, (5) 16, (6) 0, (7) 75, (8) 0, (9) 7, (10) 16, (11) 42, (12) 42, (13) 25, (14) 4, (15) 60, (16) 59, (17) 24, (18) 33, (19) 95, (20) 65, (21) 26, (22) 15, (23) 7. Random samplings of the fecal pellets of other snails also showed the presence of discarded teeth.

Further evidence for the theory that the radula is constantly growing forward (although no explanation as to how the radula passes forward is attempted here) and discarding the old worn teeth, and that the teeth in each transverse row undergo a "metamorphosis" from the primary marginal tooth to the laterals, was found in a study of the radulae of a series of consecutively older and larger laboratory snails. The shell length of the snails used varied from 5.5 to 41.0 mm. and the ages from 45 to 115 days (Table I). The tabulation in Table II shows that the median tooth remained unicuspid and constant throughout, and that the

TABLE I

Variation of Certain Characters of *L. s. appressa* with Age and with Shell Length

Characters	Snails				
Number of snail	1	2	3	4	5
Age, days	115	95	95	85	45
Shell length, mm.	41.0	23.5	18.0	10.0	5.5
Spire length, mm.	22.0	12.0	8.5	5.0	2.5
Aperture length, mm.	19.0	11.5	9.5	5.0	3.0
Aperture width, mm.	12.0	6.5	5.0	2.5	1.5
No. shell whorls	7.5	6.5	5.5	5.0	3.5
Number of transverse rows	125	103	98	74	74
Length of 1st. lateral, in μ	60	44	38	24	15
Radular dimensions, mm.	2.2×4.5	1.5×3.0	1.0×2.5	0.7×1.4	0.4×1.1
Total no. of teeth per radula	10,375	6,695	6,566	4,218	3,034

TABLE II

Variation of the Radular Formula of *L. s. appressa* with Age and with Shell Length

Types of Teeth	Number of Teeth									
Number of snail	1		2		3		4		5	
	P*	A**	P	A	P	A	P	A	P	A
Marginals	21	22	18	18	20	20	19	19	12	12
Intermediates	4–6	4–6	3	4	5	4	2	2		
									9	8
Laterals	15	15	11	10	8	8	7	7		
Median	1	1	1	1	1	1	1	1	1	1
Laterals	16	16	10	10			8	8		
					13	12			8	7
Intermediates	4–5	4–5	4	4			2	2		
Marginals	21	21	18	17	20	20	18	18	12	13

* Posterior portion of radula; ** Anterior portion of radula.

number of intermediate teeth varied only within the limits of 2 to 5. With increasing size and age of snails there was a progressive increase in the number of lateral and marginal teeth, the length of the first lateral (measured from the tip of the cone to the anterior edge of the plate of attachment), the width and the length of the radula, the number of transverse rows of teeth, and the number of teeth in any transverse row. Inspection of the form of the individual teeth through the series shows vividly the increase in the total number of teeth with age, and the "metamorphosis" of the marginals to the laterals. In the youngest snail (No. 5) no laterals were yet formed, and the radula was consequently divisible into two regions only: marginals and intermediates. The intermediates were all distinctly tricuspid and in form were about midway between the intermediate teeth and lateral teeth. In the 10 mm. snail (No. 4) the complete separation into the laterals, intermediates, and marginals had already taken place. The first lateral on either side of the median tooth persisted through all radulae examined as the tricuspid intermediate form. The right laterals and intermediates of the radula of the 18 mm. snail (No. 3) were so intermixed that the two regions could not be delimited. The nascent half of the left side of this same radula showed clearly a transition from the marginals to the intermediates in one longitudinal row of teeth; a similar transition was shown in the right side of the same radula. In the radula of the 23.5 mm. snail (No. 2) the nascent left end showed one more longitudinal row of laterals than the anterior end, thus indicating transition from the intermediate to the lateral form.

The successive teeth down any longitudinal row in a given radula do not vary perceptibly in length. The length of the individual teeth of the snail, for example of the first lateral, increases from 15 μ in a 45 day old snail to 60 μ in a 115 day old snail. This suggests a sufficient production of and subsequent discard of teeth such that the length of the teeth in any longitudinal row of the radulae of various sized snails remains fairly constant.

Summary. (1) The variation in the radular dentition in the subspecies of *Lymnaea stagnalis* mentioned here seems to make the use of radular formulae undependable, at least for subspecific diagnosis. Because of the change of the denticular pattern with the size of the snail, the radula would be a more reliable tool in classification when used with snails of known dimensions. (2) It is suggested that in the youngest snails the radula is probably formed by a few rows of marginal-like teeth produced by relatively few odontoblasts. With increase in age, the odontoblastic cushion grows laterad producing an increasing number of longitudinal rows of teeth. Each portion of the odontoblastic cushion which produces each longitudinal row of teeth progressively differentiates to produce successively the series of types of teeth found across a transverse row in the adult snail radulae. (3) Finally, there is indicated a remarkable turnover of teeth, a rate of production and discard far exceeding earlier estimates.

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NEW SPECIES OF CERION, NENIA AND DRYMAEUS

By MAXWELL SMITH

Cerion deani, new species. Plate 7, figure 7.

Shell small, subcylindric-ovate, translucent, rimate perforate, ground color cream-white, surface shining, ornamented with longitudinal chestnut colored flames which are about equal in area to the light ground. Longitudinal growth lines numerous, rather fine, slightly oblique. Spire somewhat swollen as com-